

COCOONS OF *CALLOSAMIA PROMETHEA* (SATURNIIDAE):
ADAPTIVE SIGNIFICANCE OF DIFFERENCES IN
MODE OF ATTACHMENT TO THE HOST TREE

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ABSTRACT. The cocoons of *Callosamia promethea* (Drury) (Saturniidae) are wrapped in a leaf and hang from a twig of the host tree by a silken peduncle that sheathes the leaf petiole and by a silken anchor that sheathes a variable length of the woody twig. It is proposed that in winter the cocoon's height above ground tends to protect it from mice and that its flexible attachment to a thin twig tends to protect it from woodpeckers. The anchor is usually about 2 cm long, but on thin twigs it may be much longer, sometimes extending past the next fork of the branch. The extension of the anchor seems superfluous on most of *promethea*'s hosts, trees with simple leaves where anchoring the petiole to the adjoining twig is sufficient to assure the cocoon's continued attachment to the tree after leaf fall. However, some of *promethea*'s hosts, the ashes (*Fraxinus* spp.), have compound leaves, and on these trees the cocoon will fall with the leaves in autumn unless the anchor is extended from the leaflet petiole up the rachis to encircle the adjoining woody twig.

Pupae of *Callosamia promethea* (Drury) (Saturniidae) overwinter in cocoons that dangle freely from a strong flexible silken peduncle anchored to a twig of the host tree (Fig. 1). In spinning the cocoon the larva first rolls a leaf along its midrib, fastens it at the margins, and lines it with silk to form an open-ended tube. It then spins a peduncle and anchor that are continuous with the lining of the leaf tube, the peduncle sheathing the leaf petiole and the anchor sheathing a variable length of the adjoining twig. Finally, the larva reenters the leaf-tube to spin a tough double-walled cocoon with a valve for the emergence of the adult at its top, where the petiole joins the leaf blade (Haskins & Haskins, 1958). The cocoons are usually fixed to thin terminal twigs well above the ground at the periphery of the tree's crown. They do not fall with the leaves in autumn. The enveloping leaf usually weathers away in winter, but the peduncle and anchor remain intact, securely attaching the cocoon to the tree (Ferguson, 1972).

The cocoon's height above ground probably tends to protect it from mice and its flexible attachment to a thin terminal twig, from woodpeckers. Accordingly, we present data on the predation pressure on *promethea* moth pupae, comparing it with the predation pressure, determined in other studies, on the pupae of a sympatric saturniid, *Hyalophora cecropia* (L.), whose larger cocoon often occurs in the same habitat but is immovably fixed to the stem or branch of a woody plant, usually near ground level (Scarborough et al., 1972a). We also

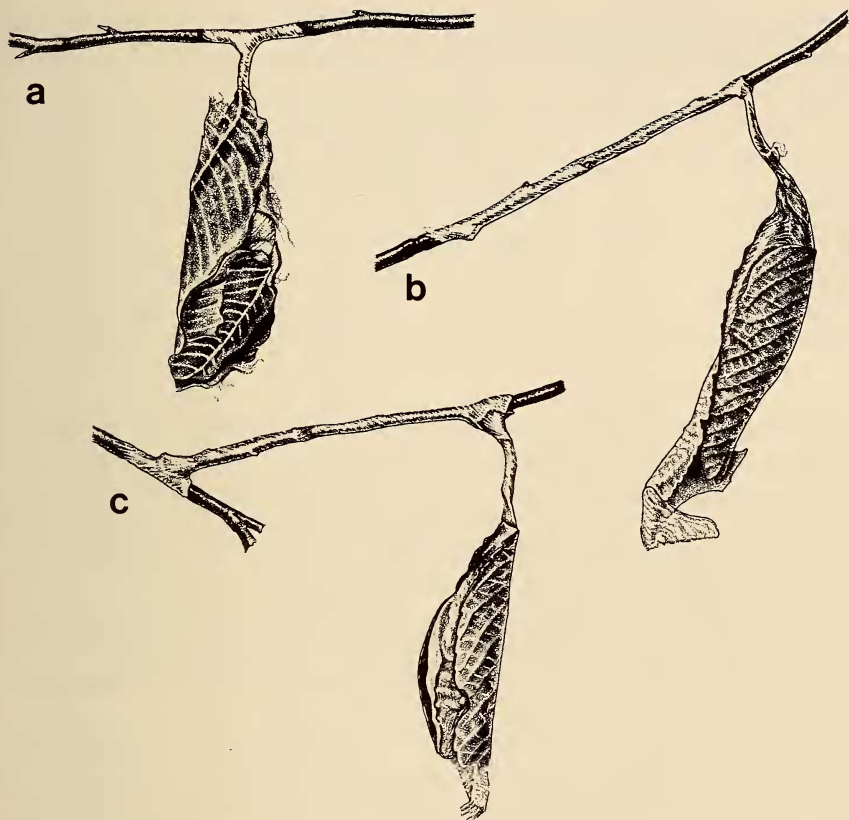


FIG. 1. *Callosamia promethea* cocoons showing the variations in the mode of attachment to the host tree. **A**, a short anchor, the usual mode of attachment; **B**, an extended anchor that does not reach past a fork; **C**, an anchor that extends past the next fork of the branch.

present data on the extent of the *promethea* cocoon's anchor. It is usually short but may be long, sometimes even extending up the twig past the first fork to sheathe a more proximal and thicker part of the branch (Fig. 1, Table 2).

MATERIALS AND METHODS

We collected *promethea* cocoons in east central Illinois from Danville south to Interstate Highway 70, and in northwestern Indiana from I-70 north to Medaryville. All were found on black cherry (*Prunus serotina* Ehrh.) or sassafras (*Sassafras albidum* Nees.) saplings that were seldom more than 3 to 4 m tall and were usually in fence rows in agricultural areas.

TABLE 1. Total *Callosamia promethea* cocoons collected, and the number and percent dead from various causes including unidentified parasites. Cocoons from Indiana were collected on 4 March 1972, and cocoons from Illinois were collected on 28 March 1972.

| | Total collected | Cause of death | | | | | | | |
|---------------------------|-----------------|----------------|-----|----------|------|------------|-----|-------|-----|
| | | Unknown | | Parasite | | Woodpecker | | Mouse | |
| | | No. | % | No. | % | No. | % | No. | % |
| Medaryville, IN | 200 | 17 | 8.5 | 4 | 2.0 | 9 | 4.5 | 1 | 0.5 |
| Reynolds, IN | 121 | 6 | 5.0 | 0 | 0 | 0 | 0 | 1 | 0.8 |
| Charleston, IL | 91 | 5 | 5.5 | 20 | 22.0 | 4 | 4.4 | 0 | 0 |
| Total or percent of total | 412 | 28 | 6.8 | 24 | 5.8 | 13 | 3.2 | 2 | 0.5 |

Random samples of *promethea* cocoons for estimates of predation pressure were collected at the localities and on the days in March shown in Table 1. Most predation had probably occurred prior to collection; Sternburg et al. (1981) found that 82.4% of the woodpecker attacks on *cecropia* moth cocoons had occurred by 4 March. Non-random samples of cocoons for determining the dimensions of the anchors and of the supporting twigs were clipped from trees with the anchor intact on 29 December 1969 near Medaryville, Indiana. We tried to find as many as possible of the relatively scarce cocoons with long anchors.

Length was measured with a rule and diameter with a micrometer. Dimensions of the distal part of the anchor (Table 2) were analyzed with a one-way ANOVA followed by the Student-Newman-Keuls test (Sokal & Rohlf, 1969). The mean lengths of the distal portions of anchors extending past the first fork (Fig. 1) cannot be legitimately compared with each other or with shorter anchors because, by definition, the lengths of the former are determined by the distance to the fork, while the lengths of the latter are not so determined.

RESULTS AND DISCUSSION

Thirteen (3.2%) of the *promethea* pupae had been killed by woodpeckers and only two (0.5%) by mice (Table 1). We found predation to be similarly light on several thousand cocoons collected in ten years at or near the same localities. However, on 1 March 1982, after two months of unusually deep snow cover, about 48% of the *promethea* cocoons that we found along 8 km of roadside near Medaryville had been attacked by woodpeckers, although *promethea* cocoons in nearby areas had not been attacked.

The similarity of the damage on these *promethea* cocoons to damage of known origin on *cecropia* cocoons leaves no doubt that the

TABLE 2. Mean length of the anchor and mean diameter of the anchor plus twig (cm \pm S.E.) of cocoons of *Callosamia promethea* collected from two host plants in the vicinity of Medaryville, IN on 29 December 1969. "Long anchor" means an extended anchor that does not reach beyond the first fork.

| | N | Distal part of anchor | | Proximal part of anchor | |
|--------------------------|----|--------------------------------|--------------------------------|-------------------------|-------------------|
| | | Diameter | Length | Diameter (twig) | Length |
| Sassafras | | | | | |
| Short anchor | 97 | 0.364 \pm 0.010 ^a | 1.419 \pm 0.048 ^a | — | — |
| Long anchor | 34 | 0.246 \pm 0.009 ^b | 5.490 \pm 0.390 ^b | — | — |
| Anchor extends | | | | | |
| Past first fork | 65 | 0.213 \pm 0.007 ^c | 5.024 \pm 0.310 | 0.417 \pm 0.018 | 1.135 \pm 0.053 |
| Wild black cherry | | | | | |
| Short anchor | 49 | 0.319 \pm 0.012 ^a | 1.581 \pm 0.072 ^a | — | — |
| Long anchor | 21 | 0.180 \pm 0.008 ^b | 7.636 \pm 0.778 ^b | — | — |
| Anchor extends | | | | | |
| Past first fork | 37 | 0.163 \pm 0.006 ^c | 4.814 \pm 0.378 | 0.366 \pm 0.022 | 1.257 \pm 0.128 |

In each column, separately for the two host plants, means not followed by the same letter are significantly different, $P \leq 0.05$.

former were attacked by woodpeckers and mice. The downy (*Dendrocopus pubescens* (L.)) and the hairy (*D. villosus* (L.)) woodpeckers pierce the cocoon, making a small hole through which their barbed tongues remove the viscous pupal contents (Waldbauer et al., 1970). Both of them are common in promethea's habitat in winter (Bent, 1964). The mice *Peromyscus maniculatus* (Wagner) and *P. leucopus* (Raf.) remove the entire pupa through a large hole which they chew in the cocoon (Scarborough, 1970; Scarborough et al., 1972b). They are also common in promethea's habitat (Hoffmeister & Mohr, 1972). We found only one type of damage that may have been caused by another predator. A few cocoons were crimped and the pupae partly crushed, as if pinched by the bill of a bird. One of us (J.G.S.) saw a blue jay (*Cyanocitta cristata* L.) in January pinch and then desert a promethea cocoon that was later found to contain only exuviae.

Although cecropia is largely urban (Scarborough, 1970) and promethea is largely rural (Sternburg & Waldbauer, unpublished), both species feed on black cherry and may occur in the same rural fence rows. We have found that cecropia cocoons often fall prey to woodpeckers and mice in this habitat.

Although we do not have comparable predation data for these two species from the same area, there is no doubt that both woodpeckers and mice generally take a far heavier toll of cecropia than of promethea. In both urban and rural areas woodpeckers regularly kill about 90% of the cecropia pupae in cocoons 45 cm or more above the ground (Waldbauer & Sternburg, 1967a, b). In rural areas mice destroy as many as 60% of the cecropia pupae near ground level (Scarborough, 1970; Scarborough et al., 1972b).

The far lower level of predation on promethea cocoons suggests that their greater height above the ground, flexible attachment to a thin twig, and perhaps their smaller size may be adaptive responses to predation by vertebrates. Although *Peromyscus leucopus* are somewhat arboreal, they rarely attack high cecropia cocoons (Scarborough et al., 1972b) or promethea cocoons (Table 1). Woodpeckers may perch directly on the large immovable cecropia cocoons (Waldbauer et al., 1970), but they are probably reluctant to perch on the far smaller and free swinging promethea cocoon. Nielsen (1977) saw a downy woodpecker hang from a promethea cocoon as it pierced the pupa, but our data (Table 1) indicate that this is uncommon. The larger hairy woodpecker may find it even more difficult to perch on promethea cocoons than does the smaller downy. The thin twigs that support promethea cocoons may not be secure perches for woodpeckers. Even if a woodpecker does find a perch near a cocoon, it may not be able to pierce it because the cocoon, hanging by its flexible peduncle, swings away

when it is pecked. About 77% of the woodpecker-attacked cocoons listed in Table 1 had been pierced down through the valve into the head of the pupa. About 34% of a sample of 38 woodpecker-attacked *Promethes* cocoons collected in 1982 had been similarly attacked. Woodpeckers may tend to attack in this way because the force of a peck directed down into the valve does not cause the cocoon to swing away.

The length of the anchor of *Promethes* cocoons varies greatly (Table 2). Those with short anchors (2 cm or less) are most common; those with long anchors (up to 19 cm) that do not extend proximad past the first fork in the twig are much less common; and those with long anchors (up to 15 cm total length) that do extend past the first fork are the least common. Note that the numbers in Table 2, not based on random samples, do not reflect the relative abundance in nature of these three anchor types.

The data in Table 2 indicate that a cue associated with the diameter of the supporting twig stimulates *Promethes* larvae to spin an extended anchor. Cocoons with anchors extending past the first fork of the twig were on the thinnest twigs, those with long anchors not extending past the fork were on somewhat thicker twigs, and those with short anchors (2 cm or less) were on the thickest twigs. The mean diameters of twigs in each category are significantly different on both black cherry and sassafras (Table 2). Whether spinning larvae extend the anchor in response to the relative thinness of the twig, or to some other property associated with thinness, perhaps greenness, cannot be determined from the data at hand. While green twigs are probably thinner than woody twigs on the same tree, they are also softer; and *Promethes* larvae may extend the anchor in response to a relatively soft-textured supporting twig.

It is reasonable to hypothesize that the extension of the anchor is intended to prevent the cocoon from falling to the ground where it can be found by mice. However, extension of the anchor on black cherry or sassafras, trees with simple leaves, seems superfluous since even a short attachment to the adjoining woody twig is sufficient to prevent the cocoon from falling with the leaves in autumn. Woody twigs seldom fall spontaneously from these trees, and there appears to be no present danger from predators that might be better able to sever a thin twig than a thick one.

We suggest that the extension of the anchor is actually an inappropriate manifestation of a behavior that evolved as an accommodation to host plants with compound leaves. The rachis of a compound leaf is green and softer than a woody twig, and it is shed in winter. The anchor must extend up the rachis to the woody twig to keep the co-

coon from falling with the leaves. The promethea host plants listed by Ferguson (1972) and Tietz (1972) include only one group with compound leaves, the ashes (*Fraxinus* spp.). We do not find promethea cocoons on ash, but Comstock and Comstock (1916) found them to be abundant on ash. Promethea may have been more common on ash, or may even have used other plant species with compound leaves, when the capacity to extend the anchor evolved. This behavior might also be adaptive on any of the willows (*Salix* spp.) that shed some of their woody twigs. Ferguson (1972) and Tietz (1972) list willows as promethea food plants, and Vestal (1913) found their cocoons abundantly on willow near Havana, Illinois.

Cocoons on wild cherry are on thinner twigs, regardless of the length of the anchor, than are cocoons on sassafras (Table 2); these differences in mean diameter are significant ($P \leq 0.05$, Student's *t* test). If we are correct in our conjecture that promethea larvae respond to green twigs by spinning a long anchor, then these differences reflect only the greater mean diameter of sassafras twigs. If, on the other hand, the larvae actually respond to thinness *per se*, then these differences suggest that the larvae compare the thickness of the supporting twig with the thinner leaf petiole or with thicker twigs traversed enroute to the spinning site.

Pammer (1966) found that another saturniid, *Samia cynthia* Drury, is adapted to cope with compound leaves. Cynthia larvae feed on *Ailanthus altissima* (Mill.) Swingle (Ferguson, 1972), a tree with large, singly compound, deciduous leaves. The caterpillars spin cocoons that, like promethea cocoons, are wrapped in a leaflet and have a peduncle extending up the petiole. Larvae of the summer generation anchor the leaflet only to the rachis; they emerge as adults before the leaves fall. Larvae of the overwintering generation, however, ensure their continued attachment to the tree by extending the anchor up the rachis to the adjoining woody twig.

Promethea is partly bivoltine in the southern part of our collecting area, but it is yet to be determined if second generation larvae are more likely to extend the anchor than are first generation larvae.

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